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Published version:

DOI:10.1071/WF15127

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Journal:	*International Journal of Wildland Fire*
Manuscript ID:	WF15127
Manuscript Type:	Research Paper
Date Submitted by the Author:	15-Jul-2015
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Keyword:	Ecosystems: temperate, Trees

Plain language summary

Trees are the dominant species in forests, which provide many ecological, economical and socio-cultural services. Because of their longevity and settledness, forest managers have to know their reaction to future climate change. In our study, we focused on beech (*Fagus sylvatica* L.), one of the most important tree species in Europe, and its species-specific reaction to forest fires.

Resilience of European beech forests (*Fagus sylvatica* L.) after fire in a global change context

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Abstract

As global climate change is predicted to affect disturbance regimes, uncertainties exist in the reaction of ecosystems historically less disturbed by fire. Marginally studied are regeneration processes in beech (*Fagus sylvatica* L.) forests, one of the most ecological and economically important tree species in Europe. Our primary object was to describe successional pathways in burnt beech forests and detect factors influencing beech regeneration. We applied a chronosequence method to study retrospective successional pathways in burnt beech forests, located in the Southern European Alps. We found abundant beech regeneration, often in co-occurrence with pioneer woody species, in fire sites of mixed burn severity. Both mutually benefited from each other until 20 years postfire when the abundance of the pioneers started to decline. Fires of mixed burn severity resulted in similar effects like after shelter-wood cuts, favouring beech regeneration in early and advanced stages under denser and lighter canopies, respectively. In contrast, high burn severity caused dense layers of early post-fire colonizers (e.g. ferns, shrubs, grass), which might delay beech regeneration for several decades. We conclude that except fires of extraordinary high burn severity, single fire events favour beech regeneration. Episodic forest fires seem therefore not to represent a major threat to the resilience of beech populations under current climatic changes.

Keywords: wildfires, beech fire ecology, burn severity, tree communities

1 Introduction

Climate change will alter future weather patterns (IPCC 2014) and might act synergistically with changes in the land-use. As one result, fire regimes are expected to react dynamically to alterations of the climate-weather-fuel system in terms of fire intensity, seasonality, frequency, and burnt area (Overpeck *et al.* 1990; Flannigan *et al.* 2000).

First signs of mentioned climatic changes are already recognizable in different fire-prone ecosystems. For instance, more and larger stand-replacing fires have disturbed forests in the western U.S. during the last 20 years (Westerling *et al.* 2006; Dennison *et al*. 2014). In western Mediterranean ecosystems, current fires are more drought-driven and less fuel limited compared to the fires before the 1970ies (Pausas and Fernándes-Muñoz 2012). Recent studies focus on changes in fire regimes in highly humanized fire-prone regions (Brotons *et al.* 2013; Luo *et al*. 2013).

However, climate and land-use change are global phenomena and fires might increasingly impact also forest ecosystems and species that are historically less prone to fire. This was for instance the case of beech forests in the Southern Alps that experienced exceptionally numerous and large fires during the hot and dry summer 2003 (Ascoli *et al.* 2013). Similarly to a majority of tree species growing in the Alps and Central Europe, beech lacks obvious fire resistance or fire-adaptation traits such as a thick bark, a strong resprouting ability, serotiny, or smoke germination cue. Thus mature beech trees are considered highly susceptible to fire (Peters 1997; Packham *et al.* 2012). Nevertheless, paleo-records of beech in the Alps demonstrate its persistence to fire on the long term, even during periods of significant increase in fire frequency (Tinner *et al.* 1999; Tinner *et* *al.* 2000). Furthermore, recent short-term studies on the postfire beech ecology indicate a good potential of beech stands to naturally regenerate after fire events (van Gils *et al.* 2010; Maringer *et al.* 2012). Observed processes of postfire beech regeneration may differ as a function of burn severity and postfire management. For instance, low to moderate burn severities increase the survivability of seed providing beech trees and result in favourable short-term germination conditions that initiate rapid beech regeneration processes (Ascoli *et al.* 2015). On the other end, severe fires cause early deaths of beech trees, which might inhibit beech regeneration (Ascoli *et al.* 2013). Unfortunately, to date, little is known about mid-term regeneration processes of beech forests disturbed by fire. Knowledge on the environmental factors triggering postfire beech regeneration processes is of paramount importance for forest managers in view of the expected general increase in fire frequency and intensity (Moriondo *et al.* 2006; Krawchuk *et al.* 2009; IPCC 2014).

In order to fill this knowledge gap, we investigated factors affecting tree regeneration in fire disturbed beech stands of the Southern foothill of the European Alps along a climatic gradient in terms of both precipitation and temperature. We used a sample of 36 beech stands burnt between 1970 and 2012 to address the following questions:

(i) Does beech successfully regenerate in burnt forest stands, i.e. how resilient is beech after fire?

(ii) Do postfire regenerating pioneer tree species limit beech regeneration?

(iii) Which are the positive and negative ecological drivers of postfire beech regeneration?

2 Material and methods

2.1 Study area

This study was conducted in the Southern Alps where a general precipitation gradient exists from the drier west (Susa in Piedmont, Italy: 07°3`0``E, 45°08`0``N, Ø temperature 12.3°C yr^{-1}, ∑ precipitation 778 mm a^{-1}; Arpa Piedmont 2015) to the wetter north-east (Locarno Monti in Ticino, Switzerland: 08°47`43``E, 46°10`12``N, Ø temperature 12.4°C a^{-1}, ∑ precipitation 1897 mm yr^{-1}; MeteoSwiss 2015; figure 1). In winter and early spring, northern foehn winds cause episodically relative humidity below 20% accompanied by significant temperature rises (Spinedi and Isotta 2005). These factors favour surface fires, mostly caused by human negligence and usually starting from the lower chestnut belt at 300–900 m a.s.l., and spreading into the adjacent beech belt at 900–1400 m a.s.l. (Valese *et al.* 2014). Prolonged droughts in the summertime are rare because dry spells do not last longer than thirty consecutive days (Isotta *et al.* 2014). Therefore, summer fires are scarce in average years, though may occur with particular intensity in case of extraordinary prolonged drought, as was the case in summer 2003 (Valese *et al.* 2014). Average summer (JJA) temperatures are around 20°C accompanied by precipitation sums of 495 mm in the Ticino and 158 mm in Piedmont, respectively (Arpa Piedmont 2015; MeteoSwiss 2015).

2.2 Selection of fire sites

Along the described precipitation gradient, we selected fire sites that potentially occurred in beech stands as registered since 1970 in the forest fire database of Switzerland (Pezzatti *et al.* 2010) and the Forestry State Corp Database of Italy (Corpo Forestale dello Stato/ Ministero delle Politiche Agricole, Alimentari e Forestali), and overlaid them with regional vegetation maps (Camerano *et al.* 2004;Ceschi 2006) using ArcGIS (version 10.0; ©ESRI). In summer 2011, we examined 94 of the selected fire sites across the following criteria: (i) burnt area of beech forest larger than 0.25 ha, (ii) no signs of additional fires during the last 50 years, (iii) no signs of wood pasture or salvage logging, (iv) no postfire artificial regeneration (plantations), (v) pre-fire stands dominated by beech with >95% of the stems, and (vi) crystalline bedrock (Gneiss, Orthogneiss; König 1967). From the examined 94 fire sites, 36 satisfied the selection criteria and were considered for the final sampling design. The topographical location of the fire sites regarding ranges in elevation (700–1500 m a.s.l.) and geography (south-west to north-east) resulted in a mean temperature and precipitation gradient from 4–9.4°C and 979–1488 mm, respectively (see appendix A). Thus, the 36 fire sites belonged to the drier and wetter bio-climatic regions of Piedmont and Insubria (Oberdorfer 1964; figure 1).

[place figure 1]

2.3 Sample and field assessment

Corresponding to the burn size, we placed one to three transects spaced 50 m apart in elevation along the contour lines (figure 2). Along the transects, circle plots of 200 m^2 were defined in distances of 30 m, starting in the burnt beech forests in 10 m distance to the burn edge. In each transect a minimum of one control plot was located beyond the edge in the unburnt beech forest, except for six fire sites where it was not possible (see appendix A). According to the final number of plots, the burn size (**AREA**; table 1) within each beech stand was categorized as small (< 4 sample plots), medium (4–9 sample plots) or large (> 9 sample plots).

Starting from the plot centre, the tree regeneration was assessed in concentric circles of variable sizes (12.5 m^2, 50 m^2, 100 m^2, 200 m^2) corresponding to the presence of at least 10 post-fire beech individuals or to a maximum circle size of 200 m^2 (figure 2). Regeneration densities were separately pooled and upscaled to stems ha^{-1} for the target species beech, and for pioneer woody species with a high annual production of wind-dispersed seeds. Remaining woody species combining traits of barochorous or zoochorous seed dispersal, and a highly variable annual seed production were summarized as “other” (table 2).

[place figure 2]

2.4 Data collection

Field survey

Between July 2012 and September 2013, a total of 234 plots were assessed in the burnt beech forests and 39 in the unburnt (control plots). Each 200 m^2-plot was characterized by slope (**SLOPE**), aspect (**ASP**), elevation (**ELE**), and micro-topography (concave, plane, convex; **TOPO**). Additionally, distances (m) were recorded between the plot centre and burnt edge (**EDGE**) and the closest uphill seed providing beech mother tree (**MOTHER**), respectively. Early postfire colonizers (**EARLY**) such as common broom (*Cytisus scoparius* (L.) LINK), common bracken (*Pteridium aquilinum* (L.) KUHN), and purple moor grass (*Molinia arundinacea* SCHRANK) were assessed in terms of their percental coverage per plot.

Coarse woody debris (**CWD**) was only considered if not disintegrated under pressure, and was then assessed following the method of Brown (1974). For this purpose, dead wood was assessed in four different diameter classes (1: 2.5–5 cm, 2: >5–7.5 cm, 3:

>7.5–15 cm, 4: >15–30 cm) along the radii of the four cardinal directions, and resulting CWD volumes per plot were finally scaled up to standard values (m^3 ha^{-1}). Mineral soil samples (N 259) were taken randomly in plots on the fire site and served to measure pH-values (**pH**; 0.01 M $CaCl_2$ solution).

Vegetation structure of pre-fire trees was determined by identifying each tree to the species level, recording the diameter at breast height (1.30 m), the tree height, and the percentage of the crown volume killed. Latter parameter was visually estimated by the volumetric proportion of crown killed compared to the space occupied by the pre-fire crown volume (Hood *et al.* 2007). All diameters at breast heights of pre-fire beeches were pooled plot-wise and scaled up to basal area (m^2 ha^{-1}).

Woody regeneration was also identified to the species level (Ammann 2005; Lauber *et al.* 2007), and categorized as seedlings (height ≤ 20 cm) and saplings (height > 20 cm). Seedlings were counted on species level separately for living and dead individuals. Saplings height and dbh (> 1cm) were measured individually for dead and living individuals.

Assessment of burn severity

Regarding the assessment of burn severity (Turner *et al.* 1997) at plot level, we faced the difficulty to estimate retrospectively severities in different aged fire events. From the various approaches existing (reviewed in Johnson and Miyanishi 2007; Keeley 2009), we selected crown volume (Lampainen *et al.* 2004) and basal area of killed trees (Larson and Franklin 2005) as components to build a severity range that is weighted by postfire years. Accordingly, we defined low burn severity independently from the burn age, if canopy loss and killed basal area of trees per plot were below 5% and 20%, respectively. Contrastingly, high burn severity was indicated by extensive canopy loss and basal area killed, both above 50% in the first postfire decade or if both parameters increased steadily to more than 90% in the following years. We assigned moderate burn severity if both canopy opening and basal area of killed trees ranged between 20% and a maximum of 90% during the whole time since the fire event.

Climate variables

Precipitation and air temperature were obtained for each fire site from the WorldClim Database (Hijmans *et al*. 2005). Average long-term sums of precipitation (**PREC**) and means of temperature (**TEMP**) refer to the period from 1950–2010. For local climatic conditions, we calculated a detrended correspondence analysis (DCA; Oksanen et al. 2015) based on tree species composition in the burnt beech forest. The first DCA-axis represents a shift from drier to wetter conditions (**TURN)**.

2.5 Data analysis

Resource needs and availability during the regeneration process change with progressive tree development. Thus for the described statistic, the fire sites were categorized together with their corresponding control plots, into different postfire age classes (Horn 1974) based on the date of fire, with "≤ 9 years", "10–15 years", "16–21 years", "22–32 years", and ">32 years".

To evaluate the influence of explanatory variables (listed in table 1) on postfire beech regeneration, we performed individual models for beech seedlings (**sFAG**) and saplings (**SFAG**). To detect the influence of fire on regeneration processes, we considered for the seedlings and saplings models only fire sites older than one and six years, respectively. Additionally to the density models, we performed a stem height model with averaged beech saplings heights (**hFAG**) at plot-level as response variable. Models were run for both the full data set (N 214), the Insubric (N 148) and Piedmont (N 66) regions to prevent a levelling of regional specific environmental parameters.

For model selection, we examined each data set for intra-class correlation (Bliese 2000). This resulted in general linear models (*GLM*) for the tree height models, and generalized mixed effect models (*GLMM*) with burn location as random factor for regeneration models (Pinheiro *et al.* 2015). Data exploration for models performing followed the guidelines of Zuur *et al.* (2010). Therefore, collinearity among covariates was detected by calculating the Pearson correlation factor as well as by the variance of inflation (VIF). Predictors were chosen according to both the ecological relevance and the precision of assessment (measurement vs. estimation). To meet the assumption of collinearity, we excluded the variables **MOTHER** (r^2 = 0.72 with **EDGE**), **REG** (r^2 =0.8 with **PREC**), and burn severity (**SEV**) from all beech regeneration models (table 1). The latter was highly correlated with the basal area of survived pre-fire trees (**BASAL**) and with the cover of early postfire colonizers (**EARLY**). For the regional specific models, we excluded **TEMP** (r^2 = -0.7 with **AGE**), and **mCLIM** (r^2 = 0.77 with **pH**, r^2 = -0.56 with **EARLY**) for Piedmont, and **TEMP** (r^2 = -0.8 with **PREC**) for Insubric models.

For model performance, regeneration densities as response variables were transformed with the Box-Cox transformation (Fox and Weisberg 2015), an often used and more general approach in ecological modelling (e.g. Krebs 1999). Continuous explanatory variables were standardized to allow model comparison between regions (Wimmer and

Dominick 2010). Both, regeneration and growth analyses were conducted by starting with variables of significant effects, and integrating additional variables and interactions. For model comparisons, we calculated the maximum likelihood (ML) and provided ANOVA tests. The best model was finally run with restricted maximum likelihood (REML) to compute standard errors and p-values of predictors (Harville 1977).

All calculations were carried out using the statistical software R Version 3.0.2 (R Development Core Team 2014).

[place table 1]

3 Results

3.1 Forest structure

Of the examined burnt beech forest plots, 14.5% were assigned to low, 44% to moderate and 40% to high-severity burns. In the burnt beech stands mean basal area of pre-fire trees survived the fires was 19.36 m^2 ha^{-1}, ranging from 2.56 m^2 to 56.1 m^2 ha^{-1}. Contrastingly, the basal area in the unburnt beech forests was in average double as high (39.4 m^2 ha^{-1}). With regard to the different classes of postfire age, basal area of living pre-fire trees in low severity fire sites ranged between 33.5 and 56.1 m^2 ha^{-1}, and was therefore up to more than ten times higher than basal area in high burn severity sites (figure 3).

[place figure 3]

3.2 Postfire tree regeneration

A total of 32 woody species were found to be regenerating in the burnt beech forests, of which 11 were also present in the unburnt forests (table 2). Out of these species, 32% showed pronounced pioneer tree traits with stem densities ranging from below 1 stems ha^{-1} up to 2343 stems ha^{-1} in the burnt beech forests, while they were totally absent in the unburnt beech forests (table 2).

The target species beech dominated in terms of densities and frequency in the burnt as well as in the unburnt forests. It regenerated in all fire sites and in 91.2% of the investigated burnt plots (table 2). Here, both seedlings and saplings grew with average densities of 7,059 and 7,233 stems ha^{-1}, respectively, which was double as high than in the unburnt beech forests. Beech regeneration was missing in only 8.8% of the burnt plots. Half of these plots burnt just the previous vegetation period and beech regeneration densities were there in general low (50–350 stems ha^{-1}). The remaining plots without beech regeneration burnt more than 10 years ago with an extraordinary high severity and display now a dense coverage of early postfire colonizers such as common bracken, common broom and purple moor grass.

Next to beech, only pioneer birch (*Betula pendula* Roth) grew also abundant in 60% of the investigated plots with an average sapling density of 2,343 stems ha^{-1}, which corresponds to one third of the beech density. In seedlings, high densities were recorded for Scotch laburnum (*Laburnum alpinum* J.Presl, Ø 4,193 stems ha^{-1}) and ash (*Fraxinus excelsior* L., Ø 2,699 stems ha^{-1}). In three fire sites with mostly high burn severity, a rare number if invasive alien plant species with pioneer character were found such as empress tree (*Paulownia tomentosa* (Thunb.) Steud.), tree of heaven (*Ailanthus altissima* (Mill.) Swingle), and black locust (*Robinia pseudoacacia* L).

[place table 2]

Temporal dynamic of tree regeneration

With view on the different postfire ages, beech seedlings densities were half as abundant (10,092 ± 2795 stems ha^{-1}) than pioneer trees during the first 9 years postfire (figure 4). The latter peaked (21,373 ± 9399 stems ha^{-1}) within this period but rapidly declined to small numbers in older fire sites. In contrast, the numbers of beech seedlings were quite similar in younger fire sites (up to 20 years) and dropped down to an average density of 2135 ± 599 stems ha^{-1} later in succession (> 32 years postfire). Saplings of beech and pioneer trees reached nearly similar densities (5812 ± 1978 and 7515 ± 1667 stems ha^{-1}) ten to fifteen years postfire. In correspondence to pioneer seedlings of the first decade postfire, saplings densities peaked ten to fifteen years postfire and steadily decreased later in succession. Beech saplings were consequently most abundant in older fire sites, i.e. 22–32 years postfire and >32 years postfire, with values of 14,256 ± 4424 and 9372 ± 2070 stems ha^{-1}, respectively. In comparison to the burnt beech stands, beech regeneration was less abundant in the unburnt beech forests with percentages from 10% to 28% (figure 4). Regeneration densities of other trees played a subordinated role in both the burnt and unburnt beech forests.

[place figure 4]

Regeneration height

The height of pioneer and beech regeneration rapidly increased after forest fires (figure 5). Pioneer trees were two to six times taller than beech saplings, but both were nearly similar in height in the period from 32 years postfire. In the unburnt beech forests, regenerating beech trees reached heights between 1.3 ± 0.32 m and 2.18 ± 0.65 m, and were therefore only half the size of those in the burnt beech forests in the late successional stages.

The *dbh* of pioneer species increased faster in comparison to beech trees. Pioneers reached an average *dbh* of 3.3 cm in 16–20 years old burnt beech forests, which correspond to a growth rate of 1 cm per postfire age class. In fire sites of the same age, *dbh* of beech regeneration amounted to only 30-50% of the pioneer dbh.

[place figure 5]

3.3 Drivers of postfire beech regeneration

With view on the different regeneration stages (seedlings vs. saplings), seedlings generally grew denser under a closer canopy of living pre-fire beeches, but were mainly restricted by denser cover of early postfire colonizers (common bracken, common broom, purple moor grass) (table 3). Next to those general factors, the full model indicated significant regional differences due to the positive correlation with the amount of precipitation (PREC). In particular in the Insubric region, seedlings densities were negatively correlated with aspect (higher on north to east facing sites), postfire age (AGE; higher in younger burnt beech forests), and with the distance to the burn edge (EDGE; higher closer to intact forests). The best model explained 64% of the variation (deviance D^2) in beech seedlings densities. In the Piedmont, seedling regeneration of beech was positively correlated (quadratic term) to soil pH (higher densities with increasing pH) and elevation (ELE). The linear term of the latter was negatively correlated with beech seedlings densities (high densities on intermediate elevation). The overall model for the Piedmont explained 55% of the variation in seedlings density.

The cover of early post-fire colonizer and basal area of living pre-fire beeches also showed a significant influence on beech saplings densities. In contrast to the seedlings models, however, the basal areas of living pre-fire beeches were negatively correlated with the saplings density (higher under smaller canopy cover). In accordance with the seedling models, sapling densities were negatively correlated with early postfire colonizer. Additionally, the overall beech sapling densities showed a significant positive correlation with the volume of coarse woody debris. In the Insubric region, beech sapling densities were positively correlated with postfire age and negatively with elevation, with a total of 32% explained variation in stem density. For the Piedmont region, sapling density was negatively correlated with aspect. Together with the mentioned general variables BASAL, EARLY and CWD, the best model for this region explained 63% of the variation in saplings stem density.

[place table 3]

Height growth of beech saplings was generally improved by the height of non-beech regeneration, as revealed by a high positive correlation (table 4). In Insubria, beech height was also significantly and positively correlated with postfire age (taller in older burnt beech forests), and negatively correlated with basal area of living pre-fire beeches (taller under lighter canopy). The best Insubric model explained 72% of variance in beech sapling heights. In the Piedmont, beech sapling heights were positively correlated with elevation (ELE) and the distance to the burns edge (EDGE; taller with increasing distance). In contrast, soil pH and the quadratic term of early post-fire colonizers (EARLY) showed slightly negative correlations. The overall sapling growth model for Piedmont had an explanatory power of 70%.

[place table 4]

4 Discussion

4.1 Presence of beech regeneration

Our results suggest that beech starts to regenerate soon after fire disturbance, which confirms the conclusions of short-term studies in burnt beech forests (Van Gils *et al.* 2010; Maringer *et al.* 2012; Ascoli *et al.* 2013; Ascoli *et al.* 2015). The high variability in beech regeneration densities found during different successional stages is comparable to results from shelterwood and wind-throw research. For example, the number of natural beech regeneration ranged from 10,000–70,000 stems ha^{-1} in a managed forest six years after canopy opening (Mountford *et al.* 2006; Barna 2011), while regeneration densities were even double as high four years after a mast (Bílek *et al*. 2009).

As beech regeneration was abundant during all successional stages, we infer that they represent in most cases a solid basis for new forests (Olesen and Madsen 2008). Plots with no beech regeneration were found in one-year-old fire sites that lacked a seed mast year and where regeneration processes have not yet started (Johnson and Miyanishi 2007). Lacking beech regeneration in older burnt beech forests related to high burn severity, where dense layers of early postfire colonizers had accumulated (common bracken, common broom and purple moor grass).

4.2 Interaction between pioneer and beech regeneration

Pioneer woody species did not hinder beech from regenerating after forest fire. Both, beech and pioneers co-occurred in considerable abundance for 20 years. During this early growth stage, we found no evidence of competitive exclusion by pioneer woody species. On the contrary, after 20 years beech becomes dominant by eventually outcompeting other woody species. While shade tolerant beech saplings are able to grow tall under the canopy of fast growing pioneer trees and thus benefit from a nurse crop effect in terms of both shade and protection from browsers, continuous beech growth during a next phase results in an crown expansion and successful competition for light (Leder 1993; Walker 1999).

The observation of rapid beech regeneration in most plots perfectly fits the direct re-growth theory postulated by Romme *et al.* (2011). Beech forests disturbed by a single surface fire seem to recover to the pre-disturbance species composition within a short period of only 40 years. Similar successional paths of beech have been also reported in post-wind-throw studies in Central Europe (Kompa 2004; Kompa and Schmid 2005; Kramer *et al.* 2014).

4.3 Ecological drivers for beech regeneration

Limiting factors for beech regeneration

Among the factors limiting beech regeneration, we consider the abundance of early postfire colonizers such as common bracken, common broom, and purple moor grass as the most important. Beech regeneration was dense up to an intermediate abundance of early colonizers cover, but was reduced or even almost absent in case of their increasing cover. Similar effects of competitive shrubs and ferns in burnt beech forests were presented in studies from Spain (Herranz *et al.* 1996) and Piedmont (Ascoli *et al.* 2013). Indeed, bracken was detected to delay beech regeneration for several years in France (Koop and Hilgen 1987), and in Switzerland after wind-throw (Brang *et al.* 2015). Graminaceous species such as purple moor grass can also exclude beech regeneration by establishing early in spring, building dense root systems and rapidly extracting nutrients and water from the soil (Harmer 1995; Coll *et al*. 2003; Provendier and Balandier 2008).

Positive drivers for beech regeneration

In general, beech regeneration was improved under open canopy and in proximity to seed sources as indicated by the basal area of survived pre-fire trees. In particular, while a denser canopy favours beech regeneration in early stages, sapling growth improves under light (e.g. Barna 2011). Our results are consistent with those from shelterwood cuttings, where a dense shelter provides seeds for recruitments and protects seedlings from competition (Petritan *et al.* 2007). Under light shelter and towards the gap centre, sapling density and height growth improved, respectively (Mountford *et al.* 2006; Barna 2011).

Climatic factors

In the investigated fire sites, beech regeneration is not limited by climatic factors such as precipitation and temperature. Annual precipitation sums in the study region range between 778 and 1897 mm, which are above the precipitation range of beech forests in Central Europe (520 mm yr^{-1} to 1030 mm yr^{-1}; Leuschner *et al.* 2006). However, the two regions in the Southern Alps are characterized by sufficient rainfall in summer (Isotta *et al.* 2014), and soils on crystalline bedrock (Gneiss, Orthogneiss; König 1967). Thus, the synergetic effect of both rarely allows a water storage capacity below beech`s limit (< 65–70 l m^{-2}; Gärtner *et al.* 2008). Nevertheless, our results indicate denser beech regeneration on northeast rather than on southwest facing slopes, suggesting an effect of local site conditions (humidity in particular) on beech growth and eventually on beech distribution (see Ceschi 2006 for the Insubric region).

Regeneration window

Beech seedlings establish soon after a forest fire of mixed severity (van Gils *et al.* 2010; Maringer *et al.* 2012; Ascoli *et al.* 2013). Based on the long surveyed period of this study we can document an increase of beech seedlings densities up to 20 years postfire, and a decline from thereon. At the same time, beech sapling densities continuously increase. Ongoing growth of beech saplings is guaranteed if sufficient light is available. Accordingly, the regeneration window for beech is limited by light. In particular, Szwagrzyk *et al.* (2001) concluded that canopy openings are essential also for shade tolerant beech saplings regarding sapling banks. In their study, the sampling banks were up to 10 years old in a managed Polish beech forest. And Petritan *et al.* (2007) found an open regeneration window of 20 years after shelterwood cut.

However, not only the light window for sapling growth seems to be crucial for successful beech regeneration, but also availability of seeds soon after disturbance. Previous short-term studies assessed the positive effect of disturbances synchronized with masting (Madsen and Larsen 1997; Olesen and Madsen 2008; Drobyshev *et al.* 2010), and detected burn severity as a key factor in this process (Ascoli *et al.* 2015). The present study detected dense cover of early post-fire colonizers as limiting beech seed germination or seedling growth and, in contrast, a gradual canopy opening as favouring the growth of beech saplings. Both factors are controlled by burn severity, which influences the speed of the opening and thus the time frame of the regeneration window. This raises the question on environmental factors triggering the pulse of seed germination and subsequent seedlings establishment, in particular the interaction of burn severity, canopy opening, environmental factors and seed mass production, as already examined for other mast-seeding trees (Peters *et al.* 2005; Iverson *et al.* 2008; Abrams and Johnson 2013).

5 Conclusion

With the present study we contribute to the knowledge in beech fire ecology by showing successional processes over a period of 43 years postfire. We demonstrated the success of beech over pioneer woody regeneration after single forest fires of mixed burn severity. Our results therefore may explain the findings of the paleo-botanical studies of the Insubric region of persisting beech in times of increased fire frequency (Tinner and Conedera 1995; Tinner *et al*. 2000). Apart from fires with extraordinary high-severity burn, single fire disturbances are revealed to be favourable to beech stand regeneration in the Southern Alps. Either by direct regrowth or by overgrowing pioneer wood, beech regeneration processes seem acting independently from gradients in temperature and precipitation in the study region. Thus episodic forest fires might not represent a major threat to the resilience of beech populations under current climatic changes. In contrary, beech may benefit from fire disturbance, as it was already postulated in post-glacial beech migration processes (Lindbladh *et al*., 2007; Bradley *et al*., 2013).

6 Acknowledgments

This study was partially supported by the Swiss Federal Office for the Environment (FOEN). Fieldwork assistance was carried out with the support of Franco Fibbioli, Simone Giavi, Marianne Steffen, Lisa Berghäuser, and Jordi Murgadas from the Swiss Federal Institute for Forest, Snow and Landscape Research and Sven Hofmann from the university of Karlsruhe (Germany). Thanks to Adel Mohammed (MA interpreting), who took care of the English version.

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Appendix A: Investigated fire sites sorted by the climatic regions (Piedmont, Insubria) and the date of fire. Further listed: class of the burnt area (small<4 plots, medium 4-9 plots, large >9 plots), years postfire (age), Ø annual temperature (T), ∑ annual precipitation (P) (both data WorldClim), and number of plots investigated in the burnt (N_b) and unburnt beech forests (N_c).

Regions Municipality	burn size	date of fire	age	E	N	T [°C]	P [mm]	N_b/ N_c
Piedmont								
Sparone	large	28.12.80	34	382545	5030710	6	1109	16/1
Rosazza	medium	19.01.90	24	418645	5058661	5.8	1195	5/0
Corio	large	15.02.90	24	385562	5021543	7.5	989	10/2
Arola	large	04.06.97	16.5	449208	5074546	7.9	1172	13/0
Varallo	large	11.08.03	10.5	442360	5078456	7.2	1186	11/1
Condove	large	01.03.08	7	364870	5000781	7.4	979	11/1
Giaglione*	medium	03.03.12	2	341650	5001664	6.4	1067	8/1
Insubric								
Indemini	small	07.08.70	42.5	488196	5105864	6.4	1349	3/1
Minusio	small	04.11.71	41	484123	5116368	4.7	1415	2/1
Gordevio*	small	09.03.73	40	482190	5116678	6.5	1355	1/0
Moghegno	small	27.11.73	39	492538	5101434	8.3	1310	3/1
Gordola	small	28.03.76	37	490491	5116753	6.0	1365	2/1
Arbedo	large	20.03.76	37	506667	5116933	7.1	1290	13/1
Astano	small	01.01.81	32	485796	5096454	8.2	1304	2/1
Indemini	large	01.01.81	32	484488	5104578	5.5	1376	12/1
Intragna	small	04.01.87	27	477570	5112256	7.6	1318	3/0
Aurigeno	small	01.08.89	23.5	478824	5118037	8.2	1308	2/1
Mugena	medium	23.03.90	23	492683	5105828	7.1	1330	6/1
Novaggio	small	10.03.90	23	486829	5098133	5.4	1371	2/1
Avegno	small	05.05.90	23	482007	5116521	6.5	1355	2/0
Pollegio	medium	09.04.95	18	492574	5139100	5.3	1391	5/2
Tenero	small	21.04.96	17	487212	5116007	8.5	1315	3/0
Ronco s.A.	medium	15.03.97	16	477225	5110649	6.6	1349	6/1
Magadino	large	15.04.97	16	491560	5107650	6.9	1335	26/3
Sonvico	medium	03.04.97	16	501239	5101934	8.8	1300	5/2
Arbedo	small	14.11.98	14	506770	5115571	8.5	1302	3/2
Indemini*	small	19.12.98	14	488487	5106098	6.6	1347	1/1
Gordevio	large	24.04.02	11	482190	5116678	6.5	1355	13/4
Maggia	small	12.03.02	11	477394	5124084	5.7	1388	3/1
Bodio	medium	18.03.03	10	495105	5136703	4	1436	5/1
Dissimo	medium	06.04.03	11	466503	5111215	5	1402	5/1
Someo	small	06.08.03	9.5	475281	5126733	5.6	1395	3/1
Villadossola	large	16.03.05	9	440231	5098748	5.6	1305	11/1
Cugnasco	medium	03.04.06	7	494084	5114855	9.4	1317	4/1
Ronco s.A.	small	23.04.07	6	477225	5110649	6.6	1349	2/1

Druogno*	large	26.03.12	2	453207	5110682	4.8	1394	12/1

* Fire sites excluded from mixed effect models

Table 1: Explanatory variables for (mixed effect) models of beech sapling height (hFAG) and regeneration densities (sFAG, SFAG). Predictors used (x) or not used (---) in all models, or excluded from a specific model (•[i]: Insubric, •[p]: Piedmont) because of collinearity.

Explanatory variables	Abbre-viation	Unit	Models		
			hFAG	sFAG	SFAG
topography					
slope	SLOPE	%	x	x	x
aspect	ASP	°	x	x	x
elevation	ELE	m a.s.l.	x	x	x
micro-topography	TOPO	factor	---	x	x
climate and geography					
temperature	TEMP	°C	•[i]	•[ip]	•[ip]
precipitation	PREC	mm	x	x	x
light and nutrients					
soil pH	pH		---	x	x
basal area pre-fire beeches	BASAL	$m^2\ ha^{-1}$	x	x	x
coarse woody debris	CWD	$m^3\ ha^{-1}$	•[p]	x	x
shift in woody species	mCLIM		---	•[i]	•[i]
biotic factors					
non-beech density	dREG	$N\ ha^{-1}$	---	x	x
Ø non-beech height	hREG	cm	x	---	---
early postfire colonizer	EARLY	%	x	x	x
input beech seeds					
distance forest edge	EDGE	m	x	x	x
distance mother tree	MOTHER	m	---	•[ip]	•[ip]
fire related variables					
years postfire	AGE	yr	•[i]	•	•
area burnt beech forest	AREA	factor	•[i]	•[i]	•[i]
burn severity	SEV	factor	•[ip]	•[ip]	•[ip]

Table 2: Regeneration densities of woody species in the burnt and unburnt beech forests. Frequency of species presence [%] in the plots [N 234] and the presence of mother-trees (M) indicated by • are noted for the burnt forests.

	Burnt beech forest						Unburnt beech forest	
	N [ha^{-1}] saplings		N [ha^{-1}] seedlings		Plots [%]	M	N [ha^{-1}] regeneration	
Species	Ø	SE	Ø	SE			Ø	SE
Target species								
Fagus sylvatica L.	7059	992	7233	982	91	•	3042	959
Pioneers with wind-dispersal								
Betula pendula Roth	2343	353	390	70	60	•	0	0
Populus tremula L.	184	145	150	140	1	•	0	0
Laburnum alpinum J.Presl	146	62	4193	1936	9		0	0
Salix caprea L.	143	42	83	24	22		0	0
Coryllus avellana L.	63	25	9	4	7		0	0
Alnus glutinosa (L.) Gaertn.	3	3	0	0	<1	•	0	0
Ailanthus altissima (Mill.) Swingle	2	2	0	0	<1		0	0
Populus nigra L.	0	0	1	1	1		0	0
Paulownia tomentosa (Thunb.)	1	1	0	0	<1		0	0
Populus alba L.	0	0	<1	<1	<1		0	0
Robinia pseudoaccacia L.	<1	<1	0	0	<1		0	0
Other trees with barochorous /zoochorous seed dispersal								
Sorbus aucuparia L.	301	166	195	67	25	•	219	209
Sorbus aria Crantz	222	99	79	18	25	•	8	7
Fraxinus excelsior L.	196	89	2699	795	27	•	351	159
Acer opulifolium Chaix.	55	47	120	120	1		0	0
Castanea sativa Mill.	55	12	61	15	24	•	32	19
Acer pseudoplatanus L.	39	19	1012	596	17	•	59	47
Prunus avium L.	14	7	60	19	14	•	8	5
Frangula alnus Mill.	12	9	8	8	<1		0	0
Quercus petraea (Mattuschka)	11	4	35	11	11	•	3	3
Larix decidua Mill.	11	4	27	12	7	•	0	0
Picea abies (L.)	11	5	7	5	3	•	1	1
Pinus sylvestris L.	3	3	1	1	1	•	0	0
Ilex aquifolium L.	2	1	4	3	2		4	3
Pinus strobus L.	2	2	0	0	1		0	0
Juglans regia L.	2	1	0	0	<1		0	0
Acer campestre L.	1	1	3	1	1		0	0
Tilia cordata Mill.	1	1	0	0	<1		0	0
Quercus pubescens Willd.	0	0	7	5	1	•	0	0
Taxus baccata L.	0	0	1	1	1	•	3	3
Acer platanoides L.	0	0	<1	<1	<1		0	0

Table 3: Estimates (ß) and standard error (SE(ß)) of best mixed-effect models for beech seedling and sapling regeneration, using all data pooled together (Full), and separately for the regions Piedmont and Insubria. Intercept (I) and residuals (Res) of the Standard Deviation are given for the random effect. Variable names are related to those reported in table 1.

	seedlings						saplings					
	full		Piedmont		Ticino		full		Piedmont		Ticino	
D^2	54%		55%		64%		47%		63%		32%	
Variables	ß	SE	ß	SE	ß	SE	ß	SE	ß	SE	ß	SE
fixed effects												
Intercept	12.7***	1.1	11.2***	1.7	18.9***	1.7	18.4***	1.4	19.8***	2.6	13.9***	.9
BASAL	2.1***	.5	2.8***	.9	3.3**	.9	-2.3***	.6	-2.5*	1.1	-1.3*	.5
$BASAL^2$					-1.4*	.6						
$EARLY^2$	-2.0***	.4	-1.2•	.6	-2.9***	.8	-2.1**	.5	-2.9***	.7	-1.0•	.5
AGE	-3.1***	.7			-6.5**	1.5	3.5*	1.1			3.2**	.7
ASP					-2.3**	.8	-1.1*	.7	-3.1***	1.1		
EDGE					-1.3**	.8	0.8*	.6				
ELE			-0.8***	1.1							-1.9*	.7
ELE^2			0.3***	.8								
CWD							2.3***	.7	7.8**	2.1	1.1*	.7
CWD^2									-1.6**	.6		
$MICRO_2$							2.3*	1.3			0.7•	1.1
$MICRO_3$							4.3*	1.5			3.4•	1.4
$SLOPE^2$							-0.7*	.4				
PH^2			6.1**	1.1								
PREC	2.1	.9										
$PREC^2$	1.6*	.7										
AGE: $EARLY^2$					1.9**	.7						

random effect

	I	Res	I	Res	I	Res	I	Res	I	Res	I	Res
burn	2.7	5.6	5.4	6.4	5.8	6.9	4.6	7.1	5.6	6.6	1.5	5.1

Signif. codes: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘•’ 0.1 ‘ns’ 1

Table 4: Results of the generalized linear model of beech sapling height using all data pooled together (Full), or separately for the regions Piedmont and Insubria. Variable names are related to those reported in table 1.

Variables	Full		Piedmont		Insubria	
Ø height [m]	2.27		0.94		1.80	
D^2	78%		70%		72%	
	ß	SE	ß	SE	ß	SE
Intercept	4.5***	.05	4.3***	.1	4.4***	.05
hREG	0.7***	.1	0.6***	.1	0.4**	.1
AGE	0.7***	.1			1***	.1
ELE	0.4***	.1	0.4***	.1		
EDGE			0.3*	.1		
pH			-0.3***	.1		
$EARLY^2$			-0.2*	.1		
BASAL					-1.2*	.1
TEMP	0.1**	.1				
PREC	-0.01	.1				
TEMP: PREC	-0.2***	.1				
AGE: hREG	-0.3***	.1				

Signif. codes: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘•’ 0.1 ‘ns’ 1

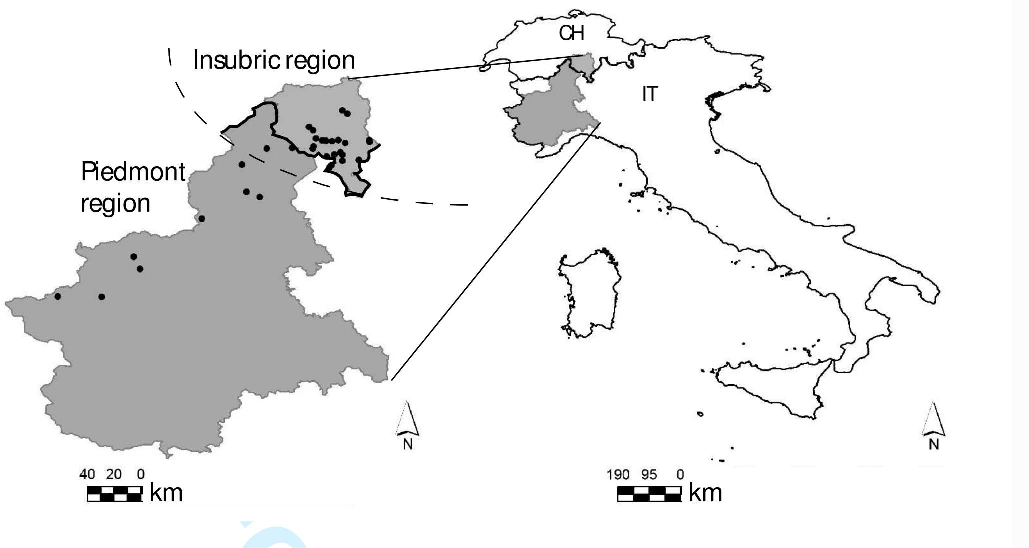

Figure 1: In grey the study region extending on the southern foothill of the Alps from the canton Ticino (Switzerland) to the Piedmont (Italy). Fire sites (black dots) in beech forests subdivided into the drier Piedmont (precipitation < 1290 mm a^{-1}) and in the wetter Insubric region (precipitation ≥ 1290 mm a^{-1}).

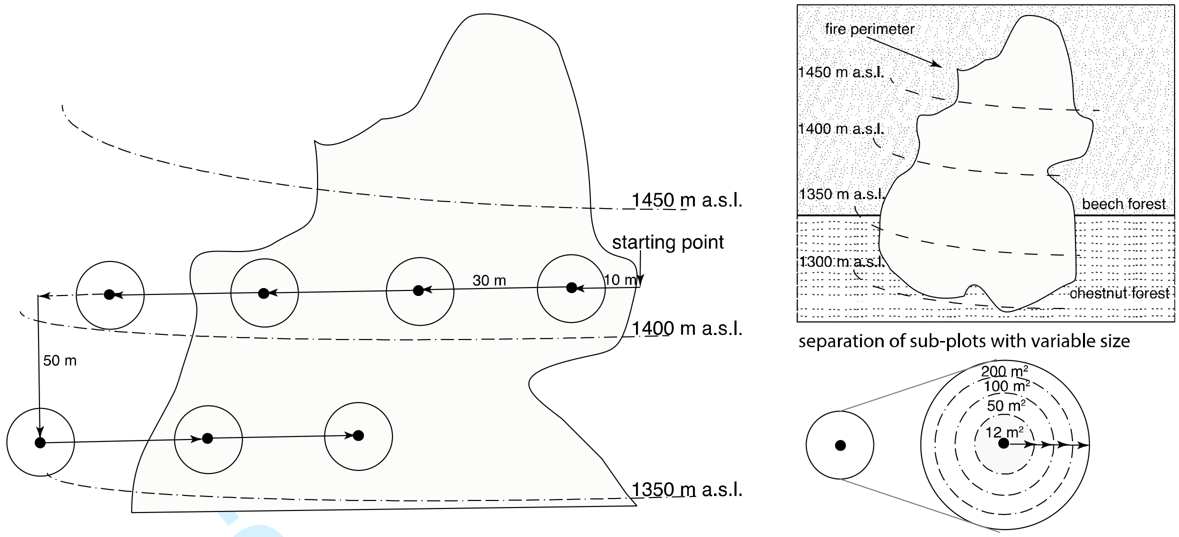

Figure 2: Sampling design in a burnt beech forest that resulted typically from fires starting in the chestnut belt and expanding upslope into the adjacent unburnt beech belt (figure top right). Circular plots of 200 m^2 were placed in 30 m distance along horizontal transects from the burnt into the unburnt beech forest (figure left), and tree regeneration was assessed in subplots of variable sizes (figure bottom right).

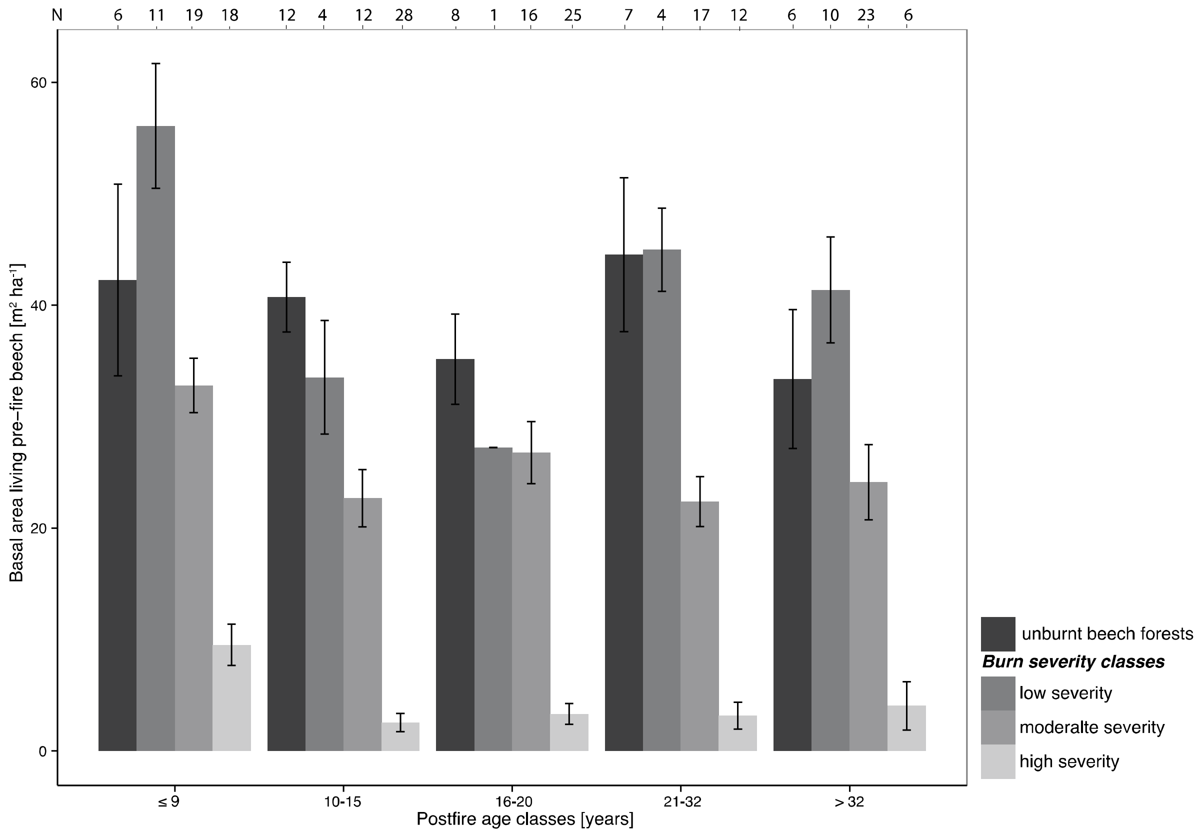

Figure 3: Basal area of living pre-fire beeches in low, moderate and high severity fire sites and the corresponding unburnt beech forests, grouped by postfire age classes.

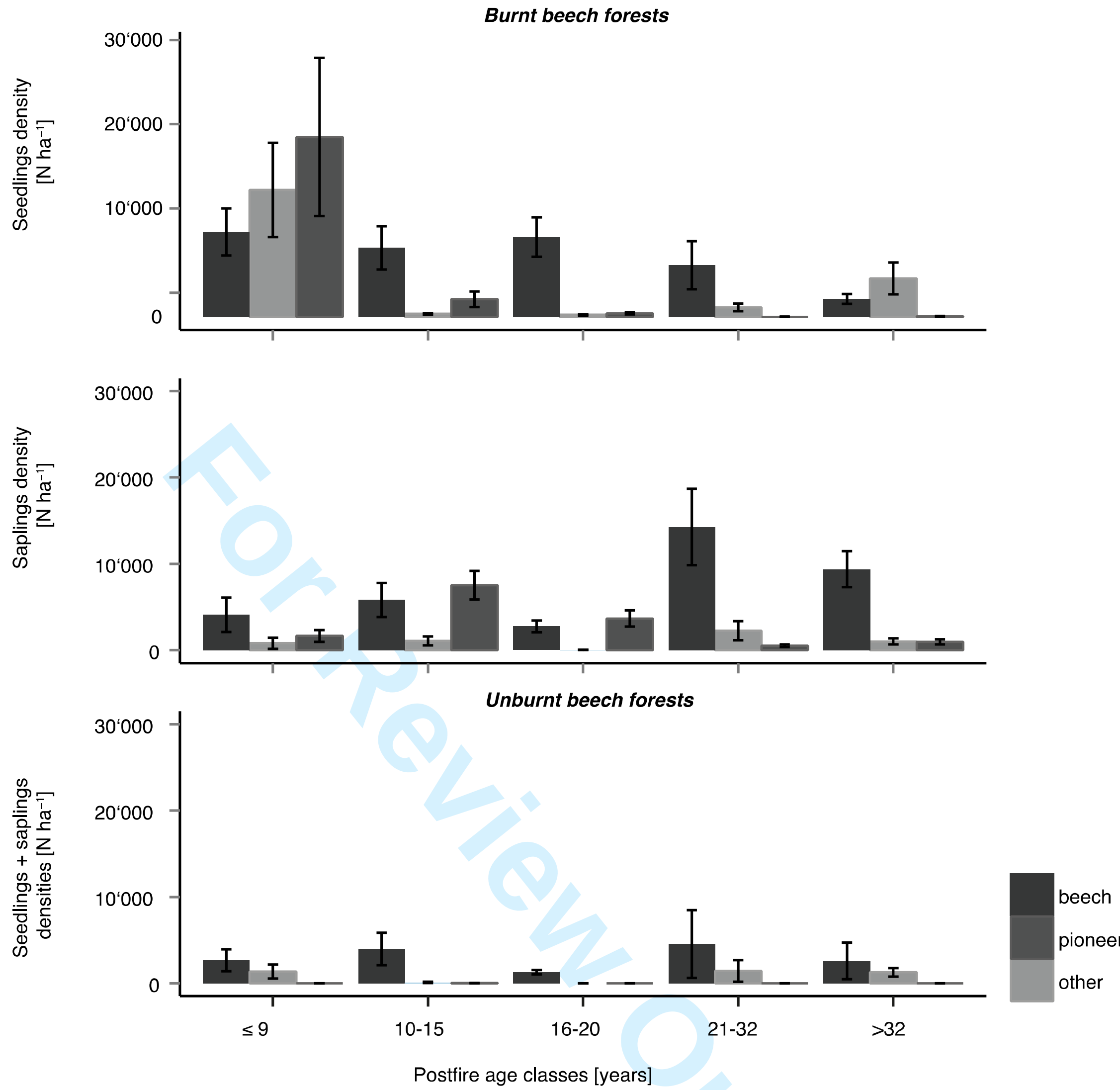

Figure 4: Regeneration densities of seedlings (≤ 20cm) and saplings (>20cm) in burnt and unburnt beech forests, grouped by beech, pioneers and other tree species, and postfire age classes.

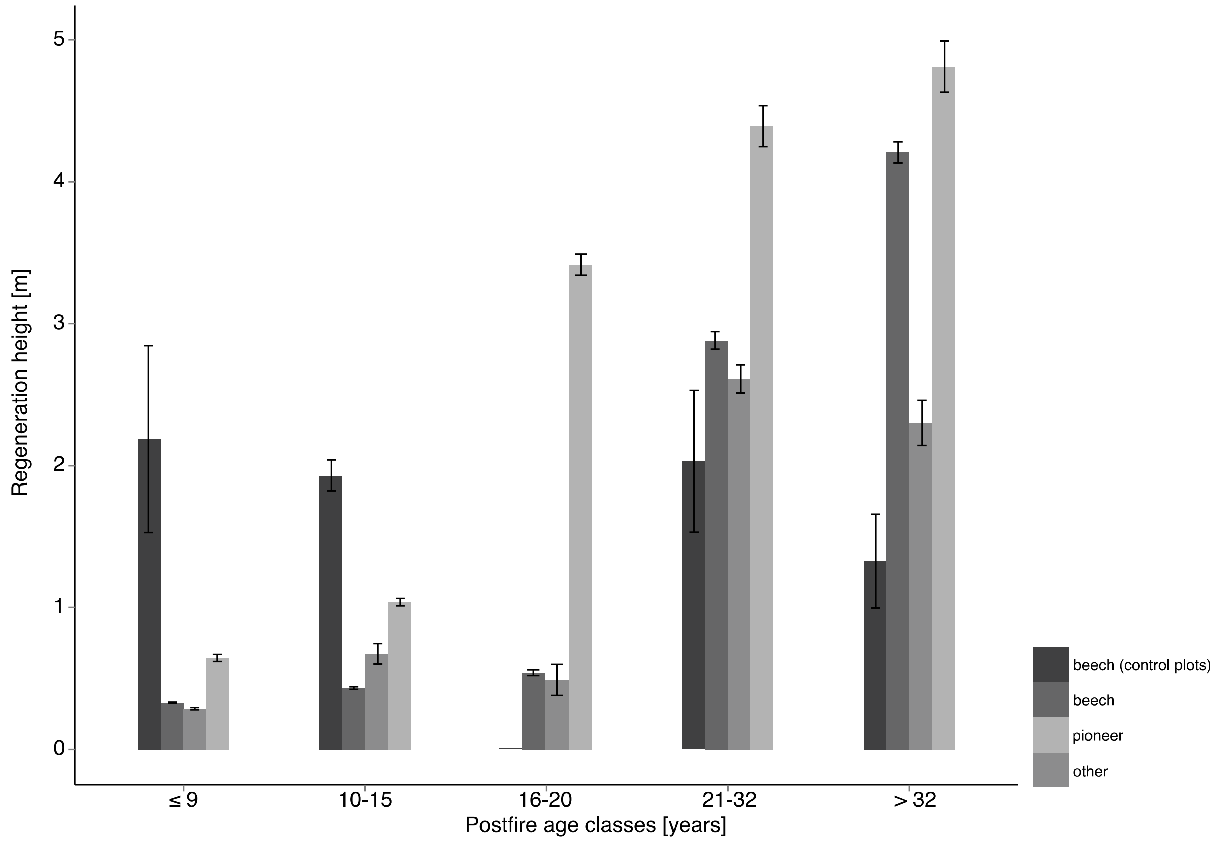

Figure 5: Saplings heights of beech, and saplings belonging to the pioneer and "other" tree species category in the burnt and unburnt beech forests, grouped by postfire age classes.